A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

NeoBiota 102: 125–150 (2025)
DOI: 10.3897/neobiota.102.148326

Research Article

Eating contest between native and non-indigenous bivalve species: estimating capture efficiencies and clearance rates using natural seston

Sara Cabral[1], Frederico Carvalho[1], Joana P. C. Cruz[1], Joshua Heumüller[1], Jose M. F. Babarro[2], Luc A. Comeau[3], Paula Chainho[1,4], Ana C. Brito[1,5]

1 *MARE–Marine and Environmental Science Centre, ARNET–Aquatic Research Network, Faculdade de Ciências, Universidade de Lisboa, 1749-016 Lisboa, Portugal*
2 *Instituto de Investigaciones Marinas CSIC, Eduardo Cabello 6, 36208 Vigo, Spain*
3 *Fisheries and Oceans Canada, Gulf Fisheries Centre, P.O. Box 5030, Moncton, E1C 9B6 New Brunswick, Canada*
4 *Escola Superior de Tecnologia, Instituto Politécnico de Setúbal, 2914-508 Setúbal, Portugal*
5 *Departamento de Biologia Vegetal, Faculdade de Ciências, Universidade de Lisboa, 1749-016 Lisboa, Portugal*
Corresponding author: Sara Cabral (sdcabral@ciencias.ulisboa.pt)

Abstract

Despite the burgeoning number of non-indigenous species (NIS) in worldwide coastal ecosystems, the quantification of their direct impacts on native communities remains largely unexplored. This is particularly true concerning feeding competition in sympatric filter-feeding bivalves. In this study, our aim was to fill a gap of knowledge on the potential trophic competition between native and non-indigenous bivalves, namely by focusing on three species that co-occur in Portuguese estuarine systems: the native cockle (*Cerastoderma edule*) and Portuguese oyster (*Magallana angulata*) and the non-indigenous Manila clam (*Ruditapes philippinarum*). The specific objectives were to i) estimate their capture efficiency (≈ particle retention efficiency; CE); ii) assess their clearance rates (CR); and iii) provide a science-based support for suitable management measures regarding NIS. Experiments were conducted in both field and laboratory conditions using the natural seston present in the seawater. The CE was higher for the larger size classes (8–14 μm) of particles measured (ranging from 4–14 μm), regardless of the species. While the individual CRs were not significantly different among species, the CR per gram of ash-free dry body tissue weight was significantly higher for the native cockle, suggesting that the NIS does not hold a competitive advantage in clearing suspended particles. However, the Manila clam might be limiting food sources availability to the native species since there is an overlap of their ecological niches.

Key words: *Cerastoderma edule*, *Magallana angulata*, Portugal, retention efficiency, *Ruditapes philippinarum*

OPEN ACCESS

Academic editor:
Tammy Robinson-Smythe
Received: 30 January 2025
Accepted: 25 March 2025
Published: 7 October 2025

Citation: Cabral S, Carvalho F, Cruz JPC, Heumüller J, Babarro JMF, Comeau LA, Chainho P, Brito AC (2025) Eating contest between native and non-indigenous bivalve species: estimating capture efficiencies and clearance rates using natural seston. In: Anastácio P, Ribeiro F, Chainho P (Eds) Invasions in Aquatic Systems. NeoBiota 102: 125–150. https://doi.org/10.3897/neobiota.102.148326

Copyright: This is an open access article distributed under the terms of the CC0 Public Domain Dedication.

Introduction

Biological invasions are considered one of the main threats to the marine environment, being a key driver of biodiversity change (Ruiz et al. 1999; Streftaris et al. 2005; Zorita et al. 2013; Jimenez et al. 2018). Non-indigenous species (NIS) have become ubiquitous across coastal ecosystems such as estuaries, bays, and coastal lagoons (Ruiz et al. 2009), since these are sheltered zones presenting a high level of anthropogenic pressure and activities (Ruiz et al. 2000). The adverse impacts of NIS are multiple and interdisciplinary ranging from economic (affecting fisheries,

aquaculture, and tourism sectors, among others; Galil et al. 2014) to ecological (including single species interactions, population declines, local extinctions, changes in community composition, and effects on entire ecosystem processes and functions; Katsanevakis et al. 2014; Anton et al. 2019).

Despite the growing knowledge about NIS impacts, this information is not yet properly addressed under the European Union legal frameworks for the protection and management of marine and freshwater ecosystems. Although temporal occurrence, abundance and spatial distribution of NIS are indicators (descriptor D2) used to assess the Environmental Status (ES) of marine waters under the Marine Strategy Framework Directive (MSFD 2008), no specific consensual tools to measure the magnitude of bioinvasion impacts have been formally adopted yet. Likewise, the indices proposed to assess the Ecological Quality Status (EQS) in transitional and coastal waters under the Water Framework Directive (WFD 2000) do not address impacts of NIS (Zaiko and Daunys 2015).

One of the potential ecological hazards posed by the introduction of NIS that should be considered in assessment tools and by decision makers is the displacement of native species (Truhlar et al. 2014). This can occur due to numerous reasons such as restricted mobility when competing for space availability (Shinen and Morgan 2009), direct predation (Battini et al. 2021), parasitism and diseases (Stiger-Pouvreau and Thouzeau 2015) or a high potential for food competition between native and NIS (Comeau et al. 2015; Nielsen et al. 2017; Sonier 2017; Rodrigues et al. 2023). Clearance rate measurements (CR; defined as the volume of water cleared of particles per unit of time) may offer insight into the potential trophic competition between suspension-feeding bivalves. An extensive CR literature spanning across decades (Møhlenberg and Riisgård 1978; Iglesias et al. 1998; Troost et al. 2009; Yu et al. 2017) revealed the sensitivity of CR values to several factors, such as temperature (Pernet et al. 2008; Cranford et al. 2011), salinity (Casas et al. 2018), distinctive experimental set-ups (Riisgård 2001), food quantity and quality (Navarro and Iglesias 1993), and contamination level at sampling sites (Widdows 2001). To date, these experiments have been conducted primarily under laboratory conditions (Møhlenberg and Riisgård 1978, 1979; Denis et al. 1999; Nakamura 2001; Haure et al. 2003; Troost et al. 2009; Joyce et al. 2019) or using artificial diets (Navarro and Widdows 1997; Petersen et al. 2004; Pascoe et al. 2009; Nagasoe et al. 2011; Tamayo et al. 2013). Nevertheless, it is recognized that laboratory CR results may deviate from *in situ* measurements (Cranford 2001; Petersen et al. 2004; Clavier and Chauvaud 2010; Rosa et al. 2018). Therefore, different species should be compared within the same trophic competition study (Troost et al. 2009), with the animals maintained under the same experimental conditions and preferably grazing on all the diversity of seston naturally available in the seawater.

Notwithstanding the vast research undertaken focusing on CR, some terms (e.g. filtration rate, retention efficiency, pumping rate, capture efficiency) have been interchangeably used (Rosa et al. 2018; Steeves et al. 2022), leading to confusion. The term retention efficiency is mostly used to refer to the proportion of particles that encounter the gill filaments and are cleared from the water, being essential to determine it before measuring a bivalve's CR (Cranford et al. 2016). Following the recommendation of Rosa et al. (2018), 'retention efficiency' will hereafter be denoted as capture efficiency (CE). This is because the number of particles that are retained by the gill can only be accurately determined if *in vivo* direct approaches are used (Shimeta and Jumars 1991; Ward et al. 1998; Rosa et al. 2018).

The non-indigenous Manila clam *Ruditapes philippinarum* is a bivalve native to the Indo-Pacific Ocean that was firstly reported in Portugal in 1984 for aquaculture purposes (Ruano and Sobral 2000). Its presence throughout European countries has been recognized to affect biogeochemical cycles and macroalgal growth (Bartoli et al. 2001) as well as causing a reduction in both density and spatial distribution area of native bivalves (Pranovi et al. 2006, ICES 2008). Furthermore, Maia et al. (2025) suggested that *R. philippinarum* holds a competitive advantage when compared with native sympatric species, not only due to its rapid growth and early sexual maturity, but also because of its broad diet and flexibility in feeding on multiple food sources according to their availability in the water column.

The purpose of the present study was to assess the potential trophic competition between native and non-indigenous bivalves feeding on natural particles. The specific objectives were to i) compare the CE of two native species (the cockle *Cerastoderma edule* and the Portuguese oyster *Magallana angulata*) and one non-indigenous species (the Manila clam *R. philippinarum*); ii) estimate their CR under field and laboratory conditions; and iii) provide a science-based support to competent authorities and regulators for suitable management measures regarding NIS.

Methods

Experimental design

To estimate the Capture Efficiency (CE) and the Clearance Rate (CR), a total of 14 experiments (seven in the field and seven in the laboratory; Fig. 1) were conducted with three species of bivalves: the native common cockle (*Cerastoderma edule*) and Portuguese oyster (*Magallana angulata*) and the non-indigenous Manila clam (*Ruditapes philippinarum*).

The field experiments took place between September 20th and October 11th, 2018, in an oyster aquaculture farm located in the Sado estuary (Setúbal, Portugal). This site is known for its wide variability of *in-situ* environmental parameters, such as temperature and salinity (AQUASADO 2022). Thus, to reduce the influence of these fluctuating variables, the experiments were also replicated in the laboratory, where conditions are inherently more stable. These experiments were conducted between the 5th and the 21st of December 2018 at the MARE-ULisboa (Lisboa, Portugal).

Field experiments

Wild specimens of *C. edule* and *R. philippinarum* were collected in an intertidal area of the Sado estuary (38°32.01'N, 8°46.85'W), while *M. angulata* individuals were obtained directly from the aquaculture farm where the experiments occurred. A set of 12 incubators (with a maximum volume of 1.2 L each) were placed on a mobile platform (Fig. 2). A single specimen of one of the selected species was placed in each incubator and three empty incubators were used as a control. Incubators were distributed randomly over the experiment platform and an air pump was attached to the wall of each incubator to homogenize the water inside them and minimize sedimentation of particles. Three replicates of each species were used per experiment. The platform was lowered to maintain the incubators permanently immersed and after 48 hours of acclimatization the experiment began by gently raising the platform with

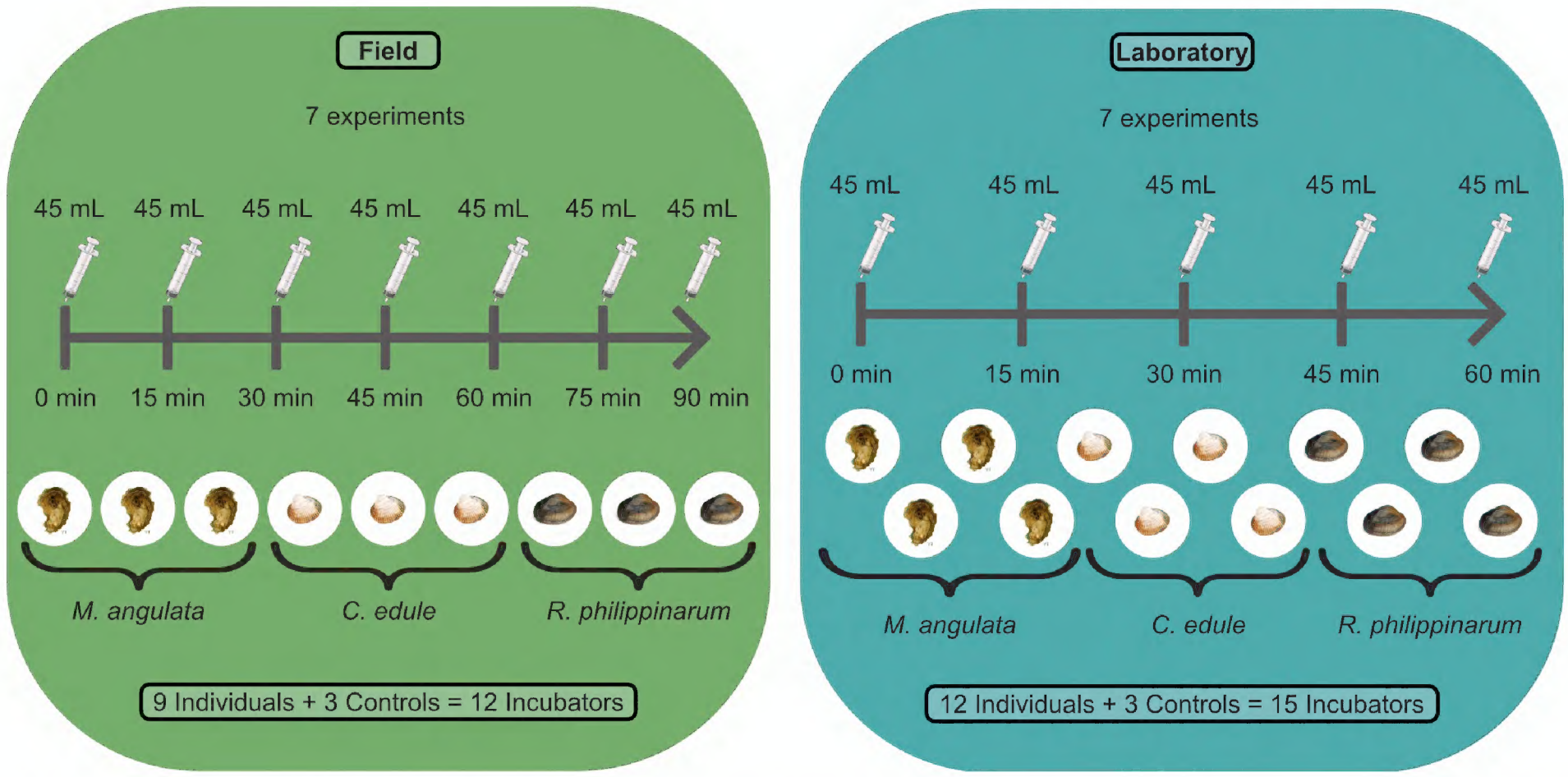
Field
7 experiments
45 mL 45 mL 45 mL 45 mL 45 mL 45 mL 45 mL
0 min 15 min 30 min 45 min 60 min 75 min 90 min
M. angulata
C. edule
R. philippinarum
9 Individuals + 3 Controls = 12 Incubators
Laboratory
7 experiments
45 mL 45 mL 45 mL 45 mL 45 mL
0 min 15 min 30 min 45 min 60 min
M. angulata
C. edule
R. philippinarum
12 Individuals + 3 Controls = 15 Incubators

Figure 1. Diagram of the water samples (volume and timings) collected in the field and laboratory experiments for the three bivalve species (*C. edule*, *M. angulata* and *R. philippinarum*).

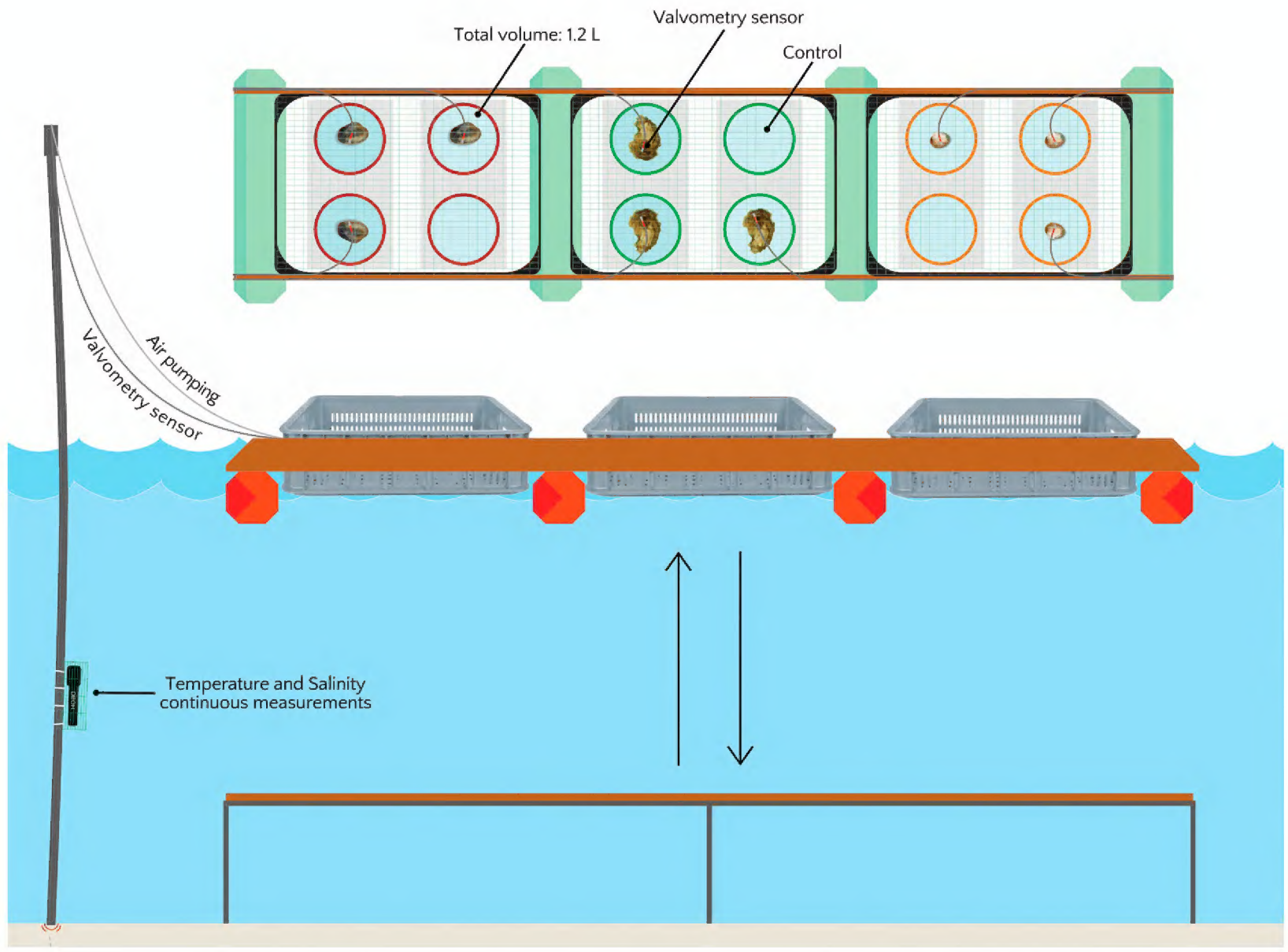

Figure 2. Experimental set-up of the field experiments, conducted in the Sado estuary (Setúbal, Portugal), using a mobile platform with incubators for three bivalve species (*C. edule*, *M. angulata* and *R. philippinarum*) and controls.

the incubators until all were isolated out of the water column. Water temperature and salinity were continuously monitored with two loggers HOBO U24 Conductivity (U24-002-C): one was positioned near the mobile platform and the other one further away at a fixed point in the water canal (Table 1).

Each experiment was conducted for 90 minutes, with water samples being collected from each incubator every 15 minutes, including a sample at T0 (time of start) and another at Tf (end time). A total of 45 mL of water was collected from each incubator at each time, preserved with 1% Lugol's Solution (Merck 109261) and subsequently stored in the dark at room temperature until further particle measurements. In addition, 15 mL of water were collected from each incubator at T0 to measure turbidity with a Lovibond infrared turbidimeter TB 210 IR (Table 1), as a proxy of the available seston load. Unpublished data measured at the same location revealed a high correlation between turbidity and suspended particulate matter (SPM; See Suppl. material 1); denoting that the average SPM during field experiments was 38.35 mg L^{-1}.

Laboratory experiments

The field experiments were replicated in the laboratory using seawater collected in the Sado estuary. Similarly, specimens of *C. edule* and *R. philippinarum* were collected in an intertidal area of the Sado estuary (38°32.01'N, 8°46.85'W), while *M. angulata* individuals were obtained directly from the aquaculture farm where the field experiments occurred. Afterwards, all animals were transported cooled with icepacks to MARE-ULisboa, where they were maintained permanently immersed for 48 hours in an aquarium to acclimate. A continuous natural seawater flow was maintained in the aquarium to ensure adequate physico-chemical conditions and food supply.

The laboratory experiments used 15 incubators (with a maximum volume of 1.2 L each) placed inside an aquarium (with 200 L of volume) with seawater (Fig. 3). Four specimens of each of the selected species (*C. edule*, *M. angulata* and *R. philippinarum*) were placed in four individual aerated incubators and three empty aerated incubators were used as control. Incubators were randomly distributed inside the aquarium. Water temperature and salinity (Table 1) were continuously monitored with one logger HOBO U24 Conductivity (U24-002-C), while dissolved oxygen and pH values were recorded daily with a multiparametric probe YSI EXO2. Additionally, the concentration of ammonia was also monitored by spectrophotometry to guarantee that it was always low.

Samples of 45 mL were taken every 15 minutes from each incubator, for a total of 60 minutes during each experiment, including a sample at T0 (time of start) and another at Tf (end time). These samples were preserved with 1% Lugol's Solution (Merck 109261) and stored in the dark at room temperature until subsequent particle measurements. In addition, 15 mL of water were also collected from each incubator during T0 (time of start) to measure the turbidity with a Lovibond infrared turbidimeter TB 210 IR (Table 1) with the aim of verifying the availability of particles. According to the correlation between turbidity and SPM (See Suppl. material 1), the average SPM during the laboratory experiments was 11.33 mg L^{-1}.

Table 1. Environmental conditions during field and laboratory experiments.

Experiment	Date	Temperature (min. – max. (°C))	Salinity (min. – max.)	Turbidity (mean ± s.d. (NTU))
Field	September to October 2018	13–20	21–25	30.88 ± 21.35
Laboratory	December 2018	15–20	22–25	6.32 ± 3.01

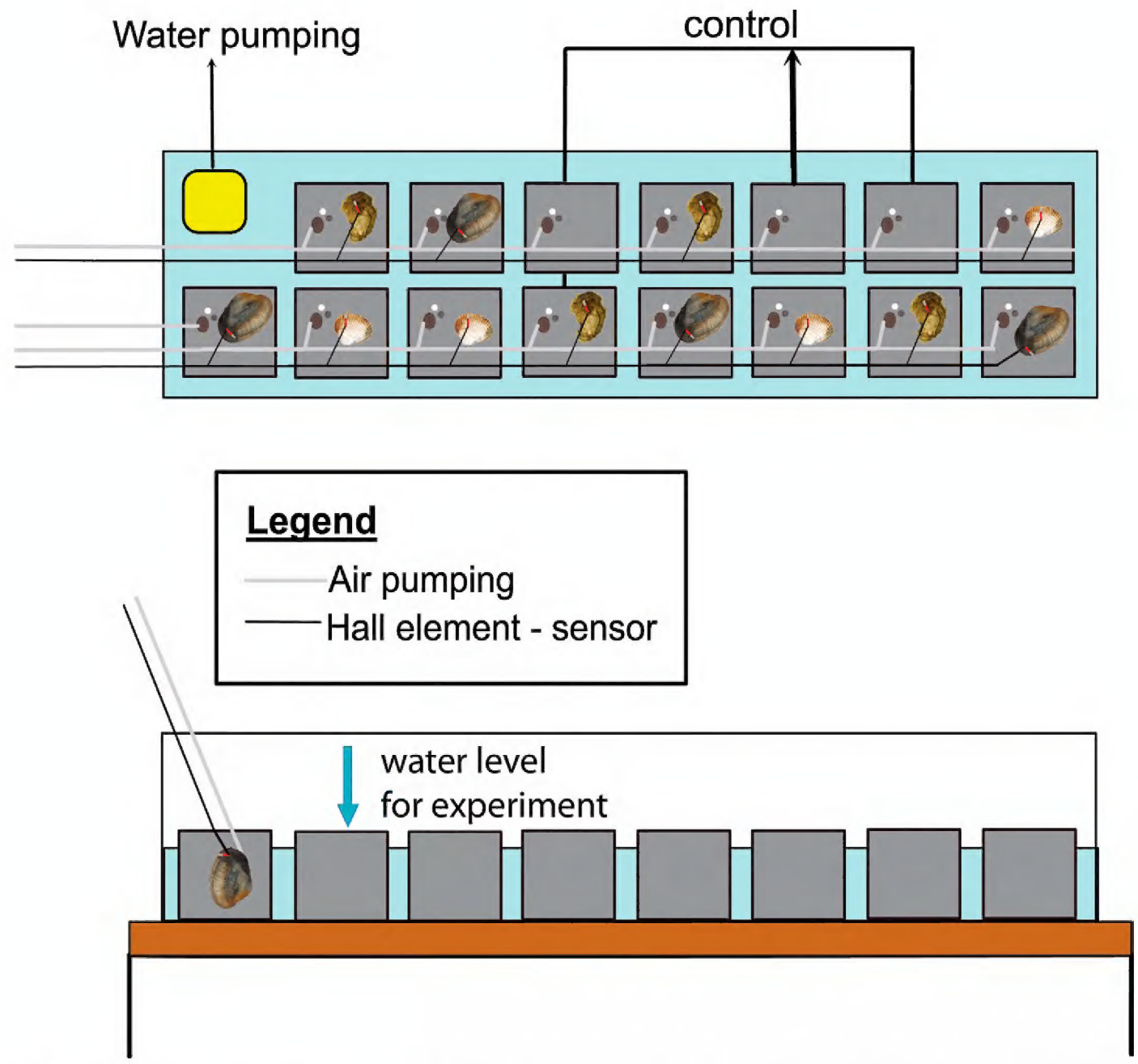

Figure 3. Experimental set-up of the laboratory experiments, conducted at the MARE-ULisboa (Lisboa, Portugal), using an aquarium with incubators for the three bivalve species (*C. edule*, *M. angulata* and *R. philippinarum*).

Valvometry

In both experiments, valve opening movements of the bivalves were recorded following a methodology described in Nagai et al. (2006) and Comeau et al. (2012). Each bivalve specimen had a coated Hall element sensor (HW-300a, Asahi Kasei, Japan) glued to one valve and a magnet attached to the other valve (directly in the opposite position of the Hall sensor), creating a magnetic field (Fig. 4). This magnetic field was recorded as output voltage by strain recording devices (DC 104R, Tokyo Sokki Kenkyujo Co., Japan) and afterwards converted into valve opening distance. These measurements allowed the identification of specimens that were completely and consistently closed during the experiments and thus, undoubtedly not interacting with their environment. These specimens were discarded from the experiments as they were presumably stressed by the manipulations. This approach minimized the potential underestimation of CR.

Estimation of the Condition Index (CI)

At the end of the experiments, all bivalves were placed in separate plastic bags, preserved in a freezer at -20 °C and stored for future analysis. Later, all specimens were processed in the laboratory: the bivalve shells were first measured and then the soft body was separated from the shell with a scalpel and tweezers, and both parts were dried at 60 °C for 72 hours, to obtain the dry weight. Lastly, the dry meat

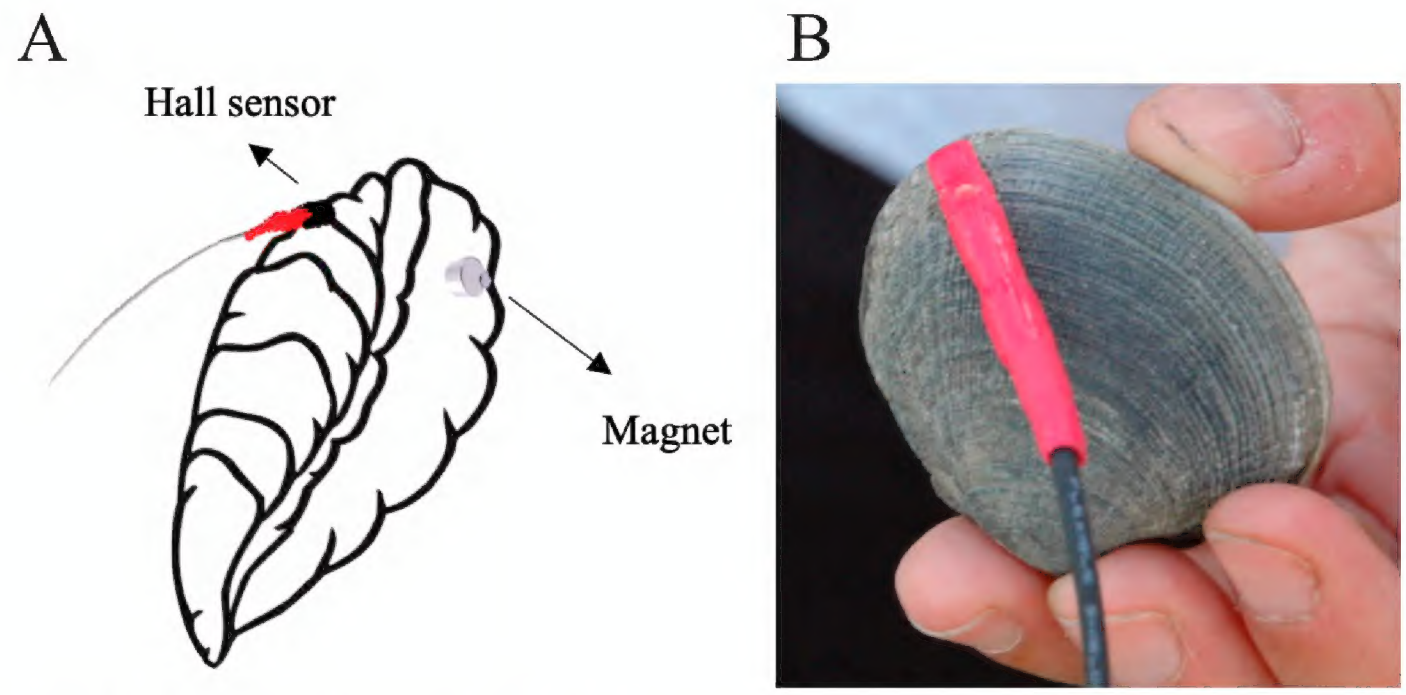

Figure 4. **A** diagram of an oyster with a Hall element sensor attached to a valve and a small magnet attached to the opposite valve **B** hall element sensor glued to the valve of a *R. philippinarum* specimen.

was burnt in a muffle furnace until weight stabilization at 500 °C, to estimate the ashes' weight. The Condition Index (CI) was calculated according to the following formula adapted from Walne and Mann (1975):

$$\text{Condition Index}(\%) = \frac{\text{Ash Free Dry Body weight}(g)}{\text{Dry shell weight}(g)} \times 100$$

The mean shell length, mean ash-free dry weight (AFDW) of the body tissue and mean condition index (CI) for each species used in field and laboratory experiments are summarized in Table 2.

Taking into consideration that the mean ash-free dry weight (AFDW) of the body tissue of the specimens varied greatly between field and laboratory experiments, data were analysed separately for each experiment type.

Estimation of Capture Efficiency (CE) and Clearance Rates (CR)

The particle count and particle size distribution were determined using a PAMAS laser particle counter (model S4031 GO) containing an HCB-LD-50/50 light-scattering sensor. Particles were counted using the light blocking principle: when the cell is 100% illuminated by laser light, the particle blocks light, and casts a shadow on a photodetector. The particle size is determined by the amount of blocked light. Control incubators were also analysed to identify any reduction in particles due to bottom deposition and adjust accordingly the incubators with bivalve specimens by subtracting this decline in particle concentration. Furthermore, these controls were also used to characterize the natural seston present in each experiment. For all experiments, the PAMAS used an initial volume of 15 mL of each water sample, in which particles were counted in 1 mL of seawater.

The PAMAS was initially set to determine 33 classes of sizes ranging from 1 to 150 µm to provide a very differentiated analysis of the sizes. However, the actual range monitored to determine both CEs and CRs was set between 4 and 14 µm due to the following: 1) the highest retention efficiency values for bivalves are attained for particles with 4 µm and above (Møhlenberg and Riisgård 1978; Cranford et al. 2016); and 2) most of the particles found in the seawater were within this size range. Otherwise, if the number of particles of a specific size is reduced,

Table 2. Mean (± SD) shell length (mm), ash-free dry body tissue weight (AFDW; g) and condition index (%) for both field and laboratory experiments of three bivalve species (*C. edule*, *M. angulata* and *R. philippinarum*).

Experiment	Species	Mean shell length (mm)	Mean AFDW of body (g)	Mean Condition Index (%)
Field	*C. edule*	31.30 ± 1.39	0.55 ± 0.24	9.61 ± 4.92
	M. angulata	85.17 ± 6.91	3.82 ± 1.55	7.60 ± 2.58
	R. philippinarum	43.57 ± 2.07	1.51 ± 0.79	10.43 ± 4.25
Laboratory	*C. edule*	29.50 ± 1.66	0.18 ± 0.02	4.12 ± 0.61
	M. angulata	91.11 ± 4.93	1.41 ± 0.20	3.16 ± 0.70
	R. philippinarum	47.09 ± 1.79	0.50 ± 0.06	4.59 ± 0.51

incorrect interpretations may be drawn, since the particles might not be captured due to its size or simply because their availability in the natural seawater is too low to be effectively captured.

The estimation of CE and CR for all species and both field and laboratory experiments followed the static method described by Cranford et al. (2016). A suspension feeder pumping at a constant rate and without water renewal will remove particles at a rate that declines exponentially (Coughlan 1969). Consequently, the PAMAS can be used to measure the slope of the natural logarithm of particle concentration decline over time (λ), taking into consideration that for all measurements, this decline should be linear over time in order to ensure the constant pumping rate assumption (Cranford et al. 2016).

The CE was estimated for each individual and each particle size according to the following equation adapted from Cranford et al. (2016):

$$CE_{\text{size}} = \frac{\lambda_{\text{sample,size}} - \lambda_{\text{control,size}}}{\lambda_{\text{sample,average}}}$$

where $\lambda_{\text{sample, size}}$ represents the slope of the linear regression between the particle concentration (transformed in natural logarithm) and the elapsed time for a given particle size class in the sample; $\lambda_{\text{control, size}}$ is the slope of the linear regression between the particle concentration (transformed in natural logarithm) and the elapsed time for the same particle size class in the control (all controls were averaged for each sampling date); and $\lambda_{\text{sample, average}}$ is the average of the $\lambda_{\text{sample, size}}$ across all particle size classes of each individual. This standardization by the average value across all particle size classes allowed to minimize the effect of potential measurement errors from a single particle size class count. The resulting CE values range from 0 to 1, representing particles sizes that are not captured and captured at maximum efficiency, respectively. Nevertheless, averaging particles across size classes, rather than using the maximum, may lead to CE values exceeding 1. Suppl. material 2 depicts an example of how some components of the CE formula were estimated for each specimen. Subsequently, the mean CE for each particle size was estimated for each species, by averaging all the individuals CE. See Table 3 for the sample sizes per species and type of experiment included in the CE estimation.

CR was estimated for each specimen, according to the equation adapted from Casas et al. (2018):

$$CR = (|\lambda_{sample} - \lambda_{control}|) \times V(L) \times 60(minh^{-1})$$

where λ_{sample} represents the slope of the linear regression between the particle concentration (transformed in natural logarithm) and the elapsed time in the sample; $\lambda_{control}$ is the slope of the linear regression between the particle concentration (transformed in natural logarithm) and the elapsed time in the control (all controls were averaged for each sampling date); and V is the volume of seawater in each incubator (1.2 L). With the aim of reducing the weight of potential outliers on the estimates of the CR, the approach of Casas et al. (2018) was followed. This method integrates the particle concentration values recorded throughout the multiple sampling times, instead of using only data from the beginning and the end of the experiments. Additionally, only linear regressions with $r^2 > 0.90$ were selected for the subsequent analyses. Suppl. material 3 depicts an example of how the CR was estimated for each specimen and Table 3 describes the number of bivalves per species and type of experiment included in the CR estimation.

Lastly, since the studied bivalve species have discrepant sizes, CR absolute values are only representative when comparing results between individuals of the same species. Hence, following the CR estimations, these values were divided by the ash-free dry weight (AFDW) of the body tissue of the respective specimen to be comparable between the different species.

Statistical analysis

The Shapiro-Wilk's and Levene's tests were used to assess the normality of residuals and the homogeneity of variances, respectively. To test for differences in CE values between species and across particle size classes a Permutational Analysis of Variance (PERMANOVA; Anderson et al. 2008) was conducted for each experiment type (field and laboratory) with Bray-Curtis similarity matrices and 9999 permutations. This analysis was performed on PRIMER® v7 (Clarke and Gorley 2015), using a two-way fixed-effect crossed design (Factors: species; particle size).

Afterwards, Kruskal–Wallis tests were used to compare the mean differences in CR between species, both for field and laboratory results. All comparisons were performed for CR (L h^{-1} ind^{-1}) and CR (L h^{-1} g^{-1} AFDW). Dunn's post hoc tests were used for pairwise comparisons between groups. Apart from the PERMANOVA, all the analyses were performed in R version 4.4.1 (RStudio version 2024.12.0).

Results

In spite of generally similar mean shell length across experiments (within each species), the mean AFDW of body tissue was always higher in field experiments, regardless of the species (Table 2). Considering this outcome, no direct comparisons between field and laboratory experiments were performed in this paper.

At the onset of the experiments, the average concentration of particles present in the seawater was estimated for each particle size (Fig. 5). Particle concentrations in the field were on average 6 to 11 times higher than in the laboratory. The maximum average number of particles per ml were recorded for the size classes of 4–5 μm (12805.12 particles ml^{-1} and 2202.87 particles ml^{-1} for field and laboratory, respectively), whereas the minimum was observed for particles within the size class of 13–14 μm (1940.39 particles ml^{-1} and 190.69 particles ml^{-1} for field and laboratory, respectively).

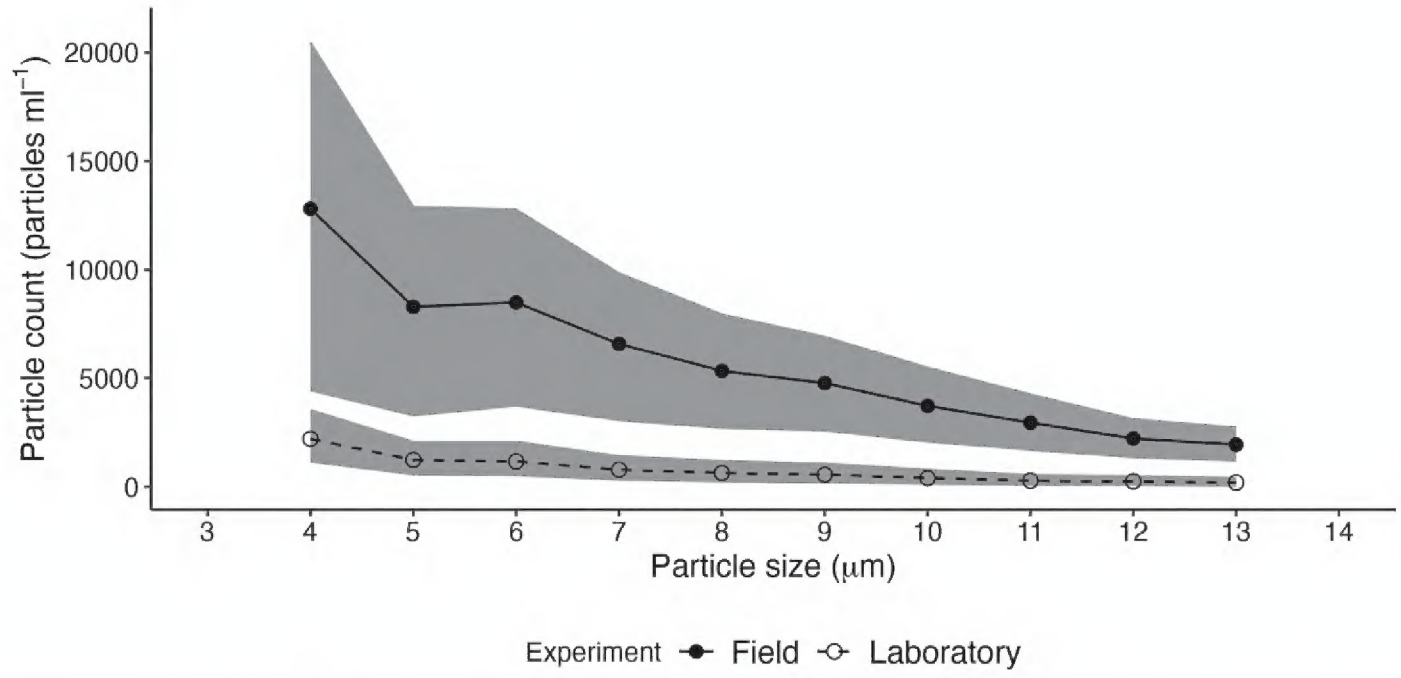

Figure 5. Number of particles per ml of seawater for each particle size for field and laboratory experiments of three bivalve species (*C. edule*, *M. angulata* and *R. philippinarum*). The black lines represent the average number of particles in all incubators at the start of the experiments and the data points represent the lower limit of each size class. The grey zones show the dispersion of data from the 10th to the 90th percentiles.

Table 3. Sample sizes included in the estimation of Capture Efficiency (CE) and Clearance Rate (CR) for both field and laboratory experiments of three bivalve species (*C. edule*, *M. angulata* and *R. philippinarum*).

Experiment	Species	Sample size used for CE†	Sample size used for CR
Field	*C. edule*	10-12	10
	M. angulata	6-8	10
	R. philippinarum	14-16	14
Laboratory	*C. edule*	15-19	20
	M. angulata	15-20	19
	R. philippinarum	15-19	23

† Since Capture Efficiency (CE) was estimated for each particle size, the reported numbers are the minimum and maximum sample sizes included in the analysis for each species.

In the field, particle size had a significant effect on CE regardless of the species (See Suppl. material 4). CE was positively related to particle size for the three species (Fig. 6A), with the smaller particles (4 to 8 µm) being associated to lower CE values compared to larger particles (8 to 14 µm; See Suppl. material 5).

CE results under laboratory conditions (Fig. 6B) were consistent with those obtained in the field (See Suppl. material 4): the absence of a species effect on CE values persisted under laboratory conditions. Moreover, as was found in the field, particle size significantly impacted CE, with particles' size classes 4–5 µm and 11–12 µm presenting the most different CE values from the remaining size classes (See Suppl. material 6). Overall, for both native and NIS species, CE tended to increase with particle size.

No significant differences ($p = 0.47$ and $p = 0.59$ for field and laboratory, respectively) were found for the average CR between species (Fig. 7A).

On the other hand, when taking into consideration the AFDW (g) of each specimen's body tissue, *C. edule* presented a significant ($p = 1.37 \times 10^{-3}$ and $p = 1.07 \times 10^{-8}$, for field and laboratory, respectively) higher CR/g for both experiments (field: 1.23 L h^{-1} g^{-1} and lab: 4.41 L h^{-1} g^{-1}), when compared with the other species (Fig. 7B). *M. angulata*, on the contrary, revealed the lowest values of CR/g (field: 0.23 L h^{-1} g^{-1} and laboratory: 0.72 L h^{-1} g^{-1}) though not significantly different

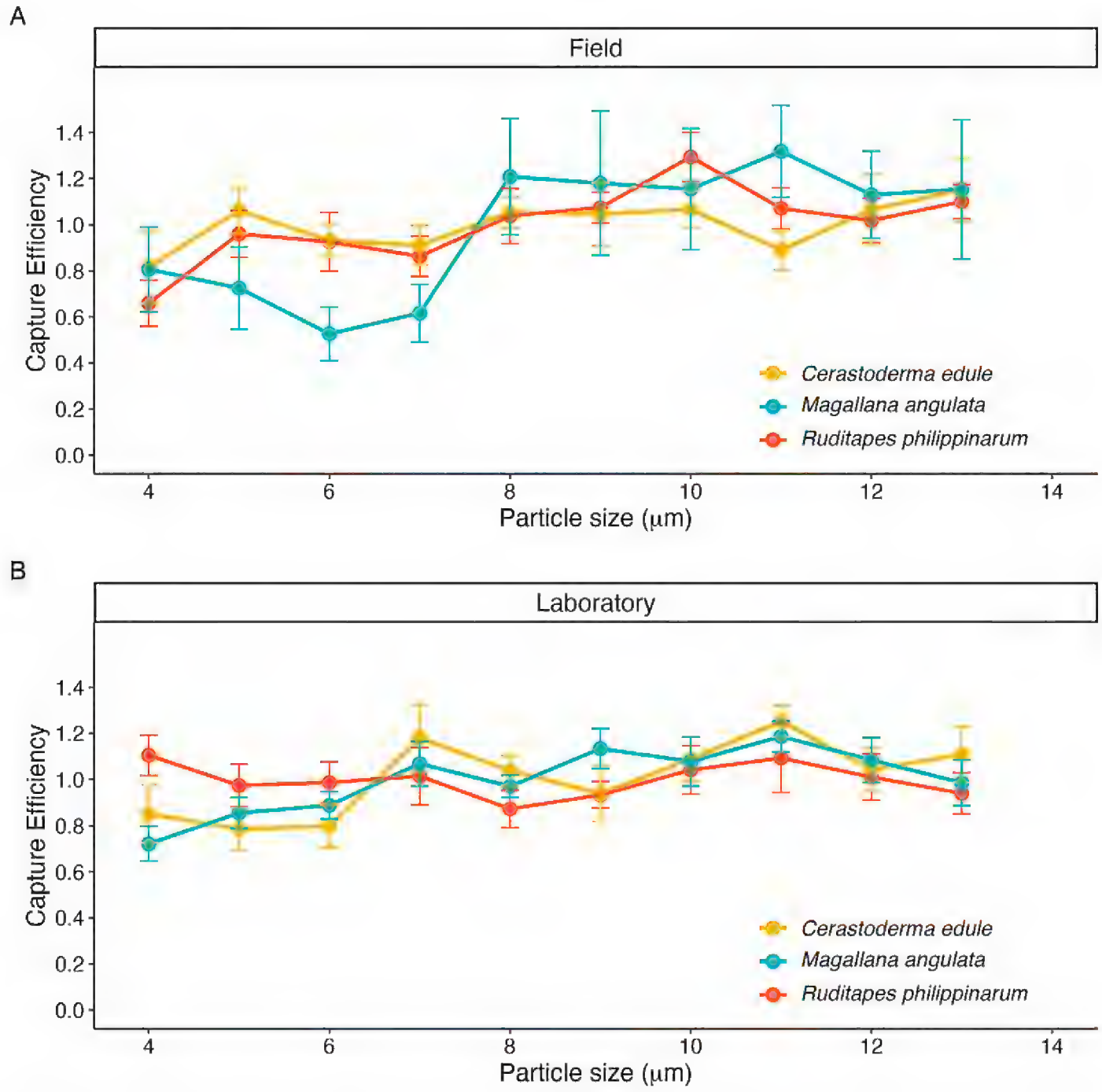

Figure 6. Capture efficiency for each particle size for **A** field and **B** laboratory experiments of three bivalve species (*C. edule*, *M. angulata* and *R. philippinarum*). The data points represent the lower limit of each size class. Bars represent the standard error.

(p = 0.51 and p = 0.06 for field and laboratory, respectively) from *R. philippinarum* (field: 0.51 L h^{-1} g^{-1} and laboratory: 1.47 L h^{-1} g^{-1}).

No statistically significant relationships were observed between CR and condition index measured in both field and laboratory experiments for any of the species (See Suppl. material 7).

Discussion

Both field and laboratory experiments were conducted using the natural seston present in the seawater and therefore provide a good demonstration of which particle sizes are naturally available in the wild environment. The number of particles available in seawater was maximum for the smallest size class measured (4–5 µm) and decreased exponentially with increasing particle size dimension, as reported for other locations (Strohmeier et al. 2012).

Early studies on various bivalve species have reported that capture efficiency generally increases in a non-linear 'plateau fashion' with the diameter of the available particles (particularly, those equal or above 4 µm; Stuart and Klumpp 1984; Jørgensen 1989; Langdon and Newell 1990). Despite the difference in particle concentrations between experiments, capture efficiency was dependent upon particle size regardless of experimental conditions.

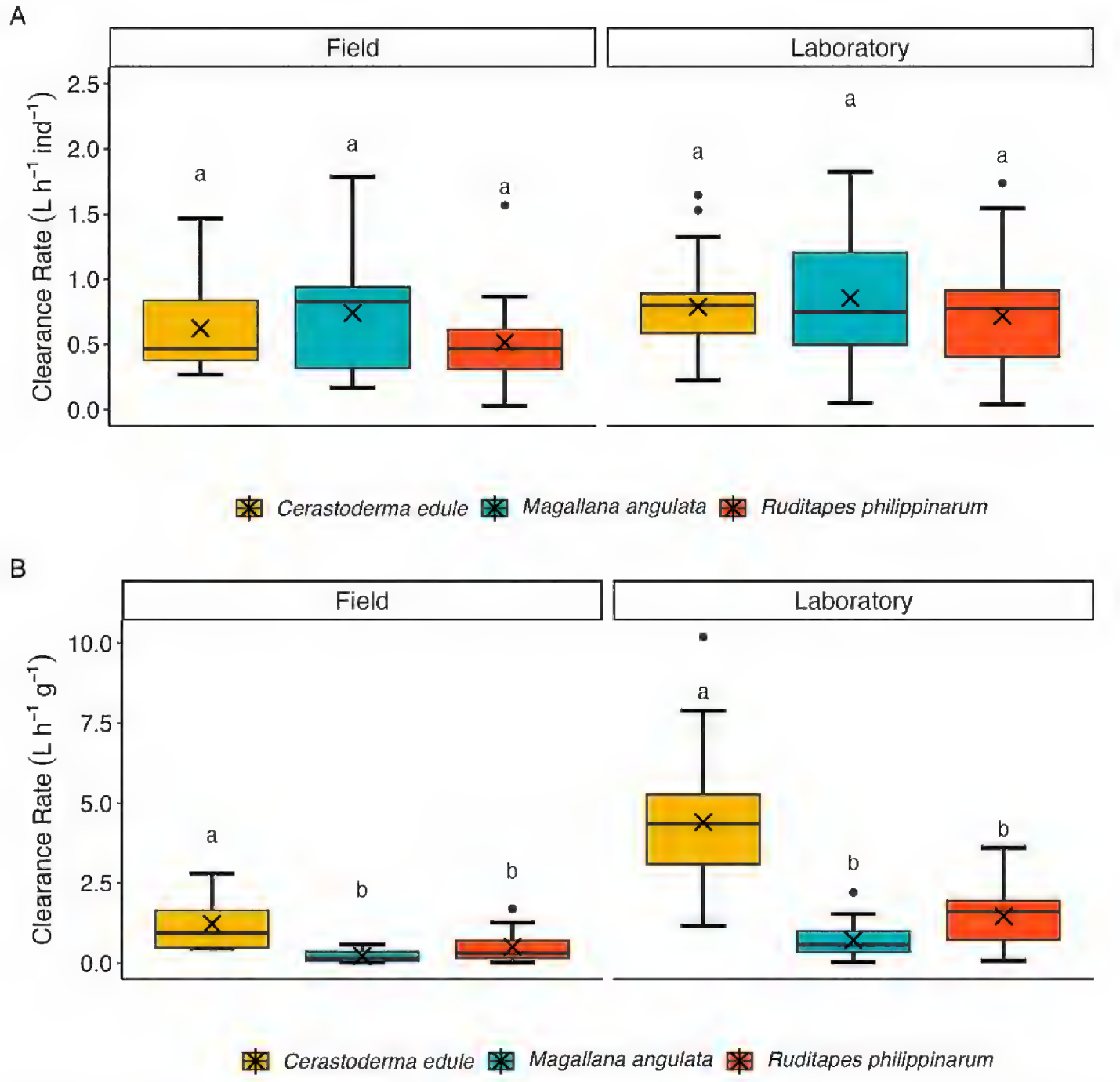

Figure 7. Clearance Rate for field and laboratory experiments of three bivalve species (*C. edule*, *M. angulata* and *R. philippinarum*) **A** clearance Rate per individual **B** clearance Rate per gram of ash-free dry body tissue weight (AFDW). Horizontal line: median; top and bottom of box: third and first quartile, respectively; lower and upper whiskers: minimum and maximum values (excluding outliers); individual point: outlier (defined as the third quartile + [1.5× the interquartile range]); cross: mean values. Statistical analyses for species comparisons conducted separately for field and laboratory experiments. Species labeled with the same letter do not differ significantly according to the Kruskal–Wallis test.

Although several previous works attempted to replicate in the laboratory the feeding conditions present in the natural environment by adding cultured microalgae with sediment particles, this approach hardly provided an accurate depiction of the field situations (Kiørboe and Møhlenberg 1981; Bricelj and Malouf 1984; Bayne et al. 1989; Navarro et al. 1992). Stenton-Dozey and Brown (1992) and Stenton-Dozey and Brown (1994) went a step further by using natural food and incorporating the respective temporal variability in their experiments, but their trials were still conducted in the laboratory. In the present study, results revealed that the capture efficiency responses of *Cerastoderma edule*, *Magallana angulata* and *Ruditapes philippinarum* were similar under field and laboratory conditions: the three species tended to more efficiently capture particles that were larger than approximately 8 μm. This outcome is consistent with the findings of Iglesias et al. (1992), who tested the selective preference of *C. edule* for particles within the range 2–12 μm. Likewise, Arakawa et al. (1998) reported a catch rate of 60% and higher for particles with sizes between 2–25 μm for *R. philippinarum*, though this study was not performed relying solely on natural water. Additionally, previous research conducted with *Ruditapes decussatus*

(a species very closely related phylogenetically) concluded that this species efficiently retained particles from 6 to 9.6 µm (with 9.6 µm being the maximum dimension assessed; Sobral and Widdows 2000). To the best of our knowledge there are no previous studies focusing on the capture efficiency (or retention efficiency) of *M. angulata*. In the present study, *M. angulata* had a highest capture efficiency for larger particles (i.e. above 8 µm), which is in agreement with the trend observed for *Crassostrea virginica* (Haven and Morales-Alamo 1970).

Higher capture efficiency does not necessarily imply higher clearance rates, since the relationship between capture efficiency and pumping rate depends on several factors, such as particle size or gill structure (Steeves et al. 2022). The average CR observed per individual was very similar across experiments and between species, with the native *M. angulata* recording a slightly higher value (0.74 L h^{-1} ind^{-1} and 0.95 L h^{-1} ind^{-1} for field and laboratory experiments, respectively). No previous works targeting the individual CR of this species were found, yet Casas et al. (2018) reported CR of 1.82 L h^{-1} ind^{-1} and 4.95 L h^{-1} ind^{-1} during winter and summer, respectively, for *C. virginica*. Even though the approach was similar to the one used in the current study (static method), the above experiments were conducted using a mixture of artificial seawater and six microalgae species, which may explain the discrepancy in the results. *Cerastoderma edule* presented an average CR of 0.62 L h^{-1} ind^{-1} and 0.79 L h^{-1} ind^{-1} for field and laboratory experiments, respectively, which is lower than other values ranging from 1.00–4.00 L h^{-1} ind^{-1} stated in the literature (Møhlenberg and Riisgård 1979; Urrutia et al. 1997; Widdows and Navarro 2007). However, the latter studies used either a different methodology to measure CR (i.e. flow-through) and/or added cultured microalgae to the bivalve's diet. Lastly, the non-indigenous *R. philippinarum* recorded the marginally lower individual CR values (field: 0.52 L h^{-1} ind^{-1} and laboratory: 0.72 L h^{-1} ind^{-1}). Similarly to the oyster, no previous research reporting individual CR values were found for the Manila clam, but Sobral and Widdows (2000) reported a higher value (1.30 L h^{-1} ind^{-1}) for *R. decussatus* clearing microalgae added to seawater. It is imperative to note that the use of cultured algae leads to higher CR than seston-based diets (Cranford et al. 2011).

Determining individual CRs is crucial for estimating the ecological carrying capacity of a specific ecosystem (Cranford 2019), since abundance data is generally the most common available type of data collected from ecological studies. Furthermore, even when biomass data is available for the ecosystem, it takes into consideration the total weight of the organisms (including the shell), whereas the CR per gram is frequently calculated with the ash-free dry tissue weight of the organism's body. This may lead to an overestimation of the Clearance Time (CT: the time needed for the bivalves to clear all the water in the ecosystem) and, consequently, to an underestimation of the clearance ratio (a ratio between CT and the water residence time (RT)). Such a situation could have severe implications when establishing aquaculture production limits, since with a clearance ratio (CT/RT) < 1, the bivalves are considered to exert a pressure on the pelagic communities through grazing, since the water is cleared faster than it is renewed (Smaal and van Duren 2019).

On the other hand, when the aim is to identify and/or quantify the potential impacts of NIS on native species by directly comparing particular species, individual CRs are not very useful mainly with species that have such divergent shell lengths, such as oysters and clams. In this case, the CR/g is the most appropriate. The native *C. edule* presented the highest CR/g (field: 1.23 L h^{-1} g^{-1} and lab: 4.41 L h^{-1} g^{-1}) regardless of the experiment. These values are consistent with the literature

findings for this species that report CR/g ranging from 1.00–3.58 L h^{-1} g^{-1} (Smaal et al. 1997; Karlsson et al. 2003; Cranford et al. 2011; Nilin et al. 2012; Ong et al. 2017). *M. angulata*, in turn, showed the lowest values of CR/g (field: 0.23 L h^{-1} g^{-1} and laboratory: 0.72 L h^{-1} g^{-1}). The scarce number of research conducted with this species and the large variation in the results, ranging from 0.009 L h^{-1} g^{-1} to 7.68 L h^{-1} g^{-1} (Mathers 1974; Haure et al. 2003; Yu et al. 2017) hamper a straightforward comparison, above all because none of the studies were conducted under similar conditions as the present one. Likewise, a low CR/g was also observed for *R. philippinarum* (field: 0.51 L h^{-1} g^{-1} and laboratory: 1.47 L h^{-1} g^{-1}), which are within the range of values referred in the literature for this species (Goulletquer et al. 1989; Nakamura 2001; Koo and Seo 2020; Jiang et al. 2023). It is also noteworthy that the interspecies CR/g patterns were similar under both experimental settings.

The high variability in the values of both CR and CR/g reported in the literature can be explained by differences in experimental set-up conditions and methodology used (Cranford et al. 2011), as well as other factors that are known to influence bivalves' filtration activity, such as temperature (Goulletquer et al. 1989; Tamayo et al. 2013), salinity (Casas et al. 2018; Barr et al. 2023), current velocity (Sobral and Widdows 2000; Karlsson et al. 2003; Fernandes et al. 2007; Widdows and Navarro 2007), contaminants (Nilin et al. 2012), food type supplied (Prins et al. 1991; Iglesias et al. 1996; Barillé et al. 1997), and even acidification (Ong et al. 2017) and hypoxia/anoxia (Sobral and Widdows 1997).

Conducting experiments under laboratory conditions to study CRs provide essential observations to fill in the existent gap of knowledge in bivalve's physiology, by controlling each variable and evaluating specific responses (Cranford et al. 2011). Nonetheless, the effects of temporal changes due to tidal influence, seasons and other variables on food quantity and quality can only be replicated in field studies (Cranford et al. 2011). In the absence of field data for a certain region, models can estimate the carrying capacity by using CR values reported in the literature from laboratory trials (Gray et al. 2022), despite the associated limitations. Not only results from different regions may vary due to geographic differences in species specific shell lengths of the bivalves or site-specific food resources available, but also individual CRs tend to be higher than average CR in a bed due to potential refiltration of the environment seawater (Troost et al. 2009). Thus, direct comparisons between native and NIS should be performed within the same study and under similar conditions, as demonstrated by several works done in recent years (Troost et al. 2009; Galimany et al. 2017; Joyce et al. 2019; Rodrigues et al. 2023).

The fact that the non-indigenous *R. philippinarum* did not reveal a higher efficiency to select and retain particles within the range 4–14 μm, when compared to the sympatric native species (*C. edule* and *M. angulata*) suggests that other biological traits may explain its success when establishing. In fact, Cardeccia et al. (2018) assessed the traits of the sixty-eight most widespread non-indigenous species in European Seas (in which *R. philippinarum* is included), determining that dispersal ability and reproductive rates are among the most associated ones.

While the native *C. edule* was the most efficient species in clearing particles from the seawater (i.e., on the basis of tissue weight), NIS nonetheless remain a menace, since their collective abundance may exert a notable pressure on the ecosystem's carrying capacity. Indeed, it is recognized that filter-feeding bivalves impact the availability of food resources to other species and directly affect the phytoplankton communities, by reducing their abundance and altering their species composition

(Prins et al. 1991; Rahman et al. 2020). Data collected in 2018 targeting bivalve communities (including the species assessed in this study; unpublished data but see Cabral et al. 2020), indicates that the average density of the non-indigenous *R. philippinarum* at the Sado estuary is higher than the average density of the native *M. angulata*, despite being very similar to *C. edule* average density (See Suppl. material 8). This pattern is even more conspicuous at the Tagus estuary, where the average density of *R. philippinarum* accounts for nearly 25% of the average density of all bivalves (See Suppl. material 8), suggesting that this NIS alone might have an important role in limiting food sources for all the remaining filter-feeding species in this ecosystem. With regards to average biomass, different species accounted for the highest observed values at the Sado and Tagus estuaries (*M. angulata* and *R. philippinarum*, respectively). This may indicate that the populations of *R. philippinarum* might be in different stages of invasion in each of the estuaries, since this species was recorded one decade early at the Tagus estuary (Cabral et al. 2020). So, a conservative approach should be adopted when analyzing the data from the Sado estuary, because this species may still be spreading in this coastal system. As a matter of fact, this seems to be the case, since the non-indigenous Manila clam has not only expanded its geographical distribution, but has also increased its total biomass by threefold between 2015 and 2019 (NIPOGES 2022). Brito et al. (2023) predicted that with an increase of 100 ha in the production area of the oyster aquaculture, a reduction of 90% in phytoplankton biomass could occur in the inner areas of the Marateca channel (Sado estuary). Considering that the total aquaculture production area in Portugal increased nearly 20% between 2020 and 2021 (INE 2023), a resource-limited scenario might be forthcoming, in which *R. philippinarum* may contribute to the potential collapse of the pelagic food web. Moreover, it was already demonstrated that *R. philippinarum* compete with native species such as *Ruditapes decussatus* and *Cerastoderma glaucum* for food resources in the Tagus estuary, since the three species rely on the same particulate sources (Dias et al. 2019). Pranovi et al. (2006) also suggested that the decreasing density of both *R. decussatus* and *C. glaucum* in the Venice Lagoon was a result of competition with the introduced *R. philippinarum*, which has been causing the displacement of several bivalve species as well as deep changes in the ecosystem functioning in this region. These alterations are even more alarming taking into consideration that NIS are unable to effectively fulfill the ecosystem functioning provided by native species, after their replacement (Steger et al. 2022).

Presently, the farming activity of *R. philippinarum* remains unregulated in Portugal, despite being exploited in the main coastal areas such as Ria de Aveiro, Tagus and Sado estuaries, as well as in Albufeira and Óbidos coastal lagoons (Chiesa et al. 2017; Moura et al. 2017). Particularly in the Tagus estuary, this led to an increase in the number of illegal harvesting activities and fishermen (Ramajal et al. 2016), representing a challenging scenario for regulators to manage. Although there are currently several regulations in place, namely establishing minimum landing sizes and maximum daily catch limits (Despacho n.° 26/DG/2024, July 24th), considerable work remains to be done, especially in terms of the involvement of key stakeholders, such as fishermen, policymakers and environmental agencies. Correia et al. (2025) reported the main results from a participatory research project focusing on *R. philippinarum* fishery in various coastal systems in Portugal, highlighting that illegal fishing is perceived by the stakeholders as a critical problem that hinders management strategies and demands higher political support.

Consequently, governing entities and regulators should be cautious when establishing new areas for bivalve aquaculture production and ensure that data on CE and CR of both native and NIS are taken into account since there is an overlap of their ecological niches. Besides, considering that the individuals used in these experiments were representative of the exploitable populations (since their shell lengths were all above the minimum marketing size), this information should also be considered when managing NIS and native species' stocks.

Conclusion

In conclusion, our results indicate that *C. edule*, *M. angulata* and *R. philippinarum* have similar capture efficiencies for the size classes of particles measured in this study (ranging from 4–14 μm). Moreover, *R. philippinarum* did not present a competitive advantage in clearing suspended particles when compared with the natives *M. angulata* and *C. edule*, with the latter revealing to be the most efficient species on a tissue weight basis. Therefore, the invasion success of *R. philippinarum* may be explained by other biological characteristics or advantages in ecological interactions such as reproductive rates, space competition or overlapping niche spaces. It is highly recommended that future studies focus on these aspects in order to provide the full extent of the potential impacts of NIS on native species. Notwithstanding, NIS may still jeopardize the entire ecosystem, by exerting an additional pressure on its carrying capacity. Finally, this study provides an important baseline contribution for the management of NIS by determining capture efficiencies and clearance rates estimated exclusively with natural seawater depicting a more accurate representation of the processes that occur in the environment.

Acknowledgements

A special thank you to Afonso Ferreira, Filipa Afonso, Inês Afonso, Inês Teodoro, Isabel Cardoso, Margarida Raposo, Marion Cottet, Pedro Coelho, Pedro Gomes, Pedro M. Oliveira, Teresa Camelo and Thomas Goulding, for assisting us during the experiments. Thanks are also due to Ramón Filgueira for the valuable suggestions. This study benefited from discussions within the Working Group on Introductions and Transfers of Marine Organisms (WGITMO) under the International Council for the Exploration of the Seas (ICES). Finally, the authors gratefully acknowledge the suggestions of the reviewers that improved the manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This work was supported by the Portuguese Foundation for Science and Technology (FCT), through the grants SFRH/BD/145746/2019 (https://doi.org/10.54499/SFRH/BD/145746/2019), 2020.06325.BD (https://doi.org/10.54499/2020.06325.BD), UI/BD/151399/2021, CEECIND/00095/2017,

2020.01797.CEECIND, UIDB/04292/2020 (https://doi.org/10.54499/UIDB/04292/2020), and the Associate Laboratory ARNET (https://doi.org/10.54499/LA/P/0069/2020). Additionally, this work was also funded by the MAR2020 projects AQUASADO (MAR-02.01.01-FEAMP-0051) and NIPOGES (MAR-01.03.02-FEAMP-0013) and by the European Union's Interreg Atlantic project COCKLES (EAPA_458/2016).

Author contributions

Conceptualization: PC, ACB. Formal analysis: SC, ACB. Funding acquisition: PC, ACB. Investigation: JH, PC, SC, FC, JPCC, JMFB, LAC, ACB. Methodology: JMFB, JPCC, FC, SC, JH, LAC, ACB. Project administration: ACB. Resources: JMFB, LAC, PC. Supervision: ACB, PC. Writing - original draft: SC. Writing - review and editing: ACB, JMFB, FC, PC, JH, JPCC, LAC.

Author ORCIDs

Sara Cabral https://orcid.org/0000-0002-7302-4105
Frederico Carvalho https://orcid.org/0000-0003-2909-0604
Paula Chainho https://orcid.org/0000-0002-3539-9942

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

References

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA + for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, UK. https://learninghub.primer-e.com/books/permanova-for-primer-guide-to-software-and-statistical-methods

Anton A, Geraldi NR, Lovelock CE, Apostolaki ET, Bennett S, Cebrian J, Krause-Jensen D, Marbà N, Martinetto P, Pandolfi JM, Santana-Garcon J, Duarte CM (2019) Global ecological impacts of marine exotic species. Nature Ecology & Evolution 3: 787–800. https://doi.org/10.1038/s41559-019-0851-0

AQUASADO (2022) Relatório Final - Promover a AQUAcultura sustentável no estuário do SADO.

Arakawa H, Yaoita T, Koike T, Morinaga T (1998) Size of suspended particles caught by Manila clam, *Ruditapes philippinarum*. Oceanographic Literature Review 7: 1179. https://www.infona.pl//resource/bwmeta1.element.elsevier-cb215dcf-ae08-324f-b0b7-119e8ecb9c46

Barillé L, Prou J, Héral M, Razet D (1997) Effects of high natural seston concentrations on the feeding, selection, and absorption of the oyster *Crassostrea gigas* (Thunberg). Journal of Experimental Marine Biology and Ecology 212: 149–172. https://doi.org/10.1016/S0022-0981(96)02756-6

Barr JM, Munroe D, Rose JM, Calvo L, Cheng KM, Bayer S, Kreeger D (2023) Seasonal Feeding Behavior of Aquaculture Eastern Oysters (*Crassostrea virginica*) in the Mid-Atlantic. Estuaries and Coasts 1: 1–16. https://doi.org/10.1007/s12237-023-01293-9

Bartoli M, Nizzoli D, Viaroli P, Turolla E, Castaldelli G, Fano EA, Rossi R (2001) Impact of *Tapes philippinarum* farming on nutrient dynamics and benthic respiration in the Sacca di Goro. Hydrobiologia 455: 203–212. https://doi.org/10.1023/A:1011910422400

Battini N, Giachetti CB, Castro KL, Bortolus A, Schwindt E (2021) New invasive predator reduces the abundance of native prey in a cold-temperate marine fouling community. Aquatic Conservation 31: 2842–2854. https://doi.org/10.1002/aqc.3681

Bayne BL, Hawkins AJS, Navarro E, Iglesias IP (1989) Effects of seston concentration on feeding, digestion and growth in the mussel *Mytilus edulis*. Marine Ecology Progress Series 55: 47–54. https://doi.org/10.3354/meps055047

Bricelj VM, Malouf RE (1984) Influence of algal and suspended sediment concentrations on the feeding physiology of the hard clam *Mercenaria mercenaria.* Marine Biology 84: 155–165. https://doi.org/10.1007/BF00393000

Brito AC, Pereira H, Picado A, Cruz J, Cereja R, Biguino B, Chainho P, Nascimento Â, Carvalho F, Cabral S, Santos C, Palma C, Borges C, Dias JM (2023) Increased oyster aquaculture in the Sado Estuary (Portugal): How to ensure ecosystem sustainability? The Science of the Total Environment 855: 158898. https://doi.org/10.1016/j.scitotenv.2022.158898

Cabral S, Carvalho F, Gaspar M, Ramajal J, Sá E, Santos C, Silva G, Sousa A, Costa JL, Chainho P (2020) Non-indigenous species in soft-sediments: Are some estuaries more invaded than others? Ecological Indicators 110: 105640. https://doi.org/10.1016/j.ecolind.2019.105640

Cardeccia A, Marchini A, Occhipinti-Ambrogi A, Galil B, Gollasch S, Minchin D, Narščius A, Olenin S, Ojaveer H (2018) Assessing biological invasions in European Seas: Biological traits of the most widespread non-indigenous species. Estuarine, Coastal and Shelf Science 201: 17–28. https://doi.org/10.1016/j.ecss.2016.02.014

Casas SM, Lavaud R, La Peyre MK, Comeau LA, Filgueira R, La Peyre JF (2018) Quantifying salinity and season effects on eastern oyster clearance and oxygen consumption rates. Marine Biology 165: 1–13. https://doi.org/10.1007/s00227-018-3351-x

Chiesa S, Lucentini L, Freitas R, Marzano FN, Breda S, Figueira E, Caill-Milly N, Herbert RJH, Soares AMVM, Argese E (2017) A history of invasion: COI phylogeny of Manila clam *Ruditapes philippinarum* in Europe. Fisheries Research 186: 25–35. https://doi.org/10.1016/j.fishres.2016.07.024

Clarke KR, Gorley RN (2015) PRIMER v7: User manual/tutorial. PRIMER-E Ltd., Plymouth, UK.

Clavier J, Chauvaud L (2010) Biodeposit production by *Bractechlamys vexillum* (bivalve: Pectinidae) in a tropical lagoon. Journal of Sea Research 64: 231–240. https://doi.org/10.1016/j.seares.2010.03.001

Comeau LA, Mayrand É, Mallet A (2012) Winter quiescence and spring awakening of the Eastern oyster *Crassostrea virginica* at its northernmost distribution limit. Marine Biology 159: 2269–2279. https://doi.org/10.1007/s00227-012-2012-8

Comeau LA, Filgueira R, Guyondet T, Sonier R (2015) The impact of invasive tunicates on the demand for phytoplankton in longline mussel farms. Aquaculture (Amsterdam, Netherlands) 441: 95–105. https://doi.org/10.1016/j.aquaculture.2015.02.018

Correia MJ, Chainho P, Goulding T, Carvalho F, Cabral S, Ferreira FG, Vasconcelos L (2025) Participatory action research supporting adaptive governance of Manila clam fisheries. Marine Policy 174: 106605. https://doi.org/10.1016/j.marpol.2025.106605

Coughlan J (1969) The estimation of filtering rate from the clearance of suspensions. Marine Biology 2: 356–358. https://doi.org/10.1007/BF00355716

Cranford PJ (2001) Evaluating the "reliability" of filtration rate measurements in bivalves. Marine Ecology Progress Series 215: 303–305. https://doi.org/10.3354/meps215303

Cranford PJ (2019) Magnitude and extent of water clarification services provided by bivalve suspension feeding. In: Smaal A, Ferreira J, Grant J, Petersen JSØ (Eds) Goods and Services of Marine Bivalves. Springer International Publishing, 119–141. https://doi.org/10.1007/978-3-319-96776-9_8

Cranford PJ, Evan Ward J, Shumway SE (2011) Bivalve filter feeding: variability and limits of the aquaculture biofilter. In: Shumway SE (Ed.) Shellfish Aquaculture and the Environment. John Wiley & Sons, Inc., Oxford, 81–124. https://doi.org/10.1002/9780470960967.ch4

Cranford PJ, Strohmeier T, Filgueira R, Strand Ø (2016) Potential methodological influences on the determination of particle retention efficiency by suspension feeders: *Mytilus edulis* and *Ciona intestinalis.* Aquatic Biology 25: 61–73. https://doi.org/10.3354/ab00660

Denis L, Alliot E, Grzebyk D (1999) Clearance rate responses of Mediterranean mussels, *Mytilus galloprovincialis*, to variations in the flow, water temperature, food quality and quantity. Aquatic Living Resources 12: 279–288. https://doi.org/10.1016/S0990-7440(00)86639-5

Despacho n.° 26/DG/2024, July 24th (2024) Despacho n.° 26/DG/2024, July 24th. https://www.dgrm.pt/documents/20143/84407/f_2796510_1.pdf/43cb5fd6-b3ac-f068-87b9-6b189057052d

Dias E, Chainho P, Barrocas-Dias C, Adão H (2019) Food sources of the non-indigenous bivalve *Ruditapes philippinarum* (Adams & Reeve, 1850) and trophic niche overlap with native species. Aquatic Invasions 14: 638–655. https://doi.org/10.3391/ai.2019.14.4.05

Fernandes S, Sobral P, van Duren L (2007) Clearance rates of *Cerastoderma edule* under increasing current velocity. Continental Shelf Research 27: 1104–1115. https://doi.org/10.1016/j.csr.2006.08.010

Galil BS, Marchini A, Occhipinti-Ambrogi A, Minchin D, Narščius A, Ojaveer H, Olenin S (2014) International arrivals: Widespread bioinvasions in European Seas. Ethology Ecology and Evolution 26: 152–171. https://doi.org/10.1080/03949370.2014.897651

Galimany E, Freeman CJ, Lunt J, Domingos A, Sacks P, Walters L (2017) Feeding competition between the native oyster *Crassostrea virginica* and the invasive mussel *Mytella charruana.* Marine Ecology Progress Series 564: 57–66. https://doi.org/10.3354/meps11976

Goulletquer P, Heral M, Deslous-Paoli JM, Prou J, Garnier J, Razet D, Boromthanarat W (1989) Ecophysiologie et bilan énergétique de la palourde japonaise d'élevage *Ruditapes philippinarum.* Journal of Experimental Marine Biology and Ecology 132: 85–108. https://doi.org/10.1016/0022-0981(89)90217-7

Gray MW, Pinton D, Canestrelli A, Dix N, Marcum P, Kimbro D, Grizzle R (2022) Beyond residence time: Quantifying factors that drive the spatially explicit filtration services of an abundant native oyster population. Estuaries and Coasts 45: 1343–1360. https://doi.org/10.1007/s12237-021-01017-x

Haure J, Huvet A, Palvadeau H, Nourry M, Penisson C, Martin JLY, Boudry P (2003) Feeding and respiratory time activities in the cupped oysters *Crassostrea gigas*, *Crassostrea angulata* and their hybrids. Aquaculture (Amsterdam, Netherlands) 218: 539–551. https://doi.org/10.1016/S0044-8486(02)00493-3

Haven DS, Morales-Alamo R (1970) Filtration of particles from suspension by the American oyster *Crassostrea virginica.* The Biological Bulletin 139: 248–264. https://doi.org/10.2307/1540081

ICES (2008) Report of the Working Group on Introduction and Transfers of Marine Organisms (WGITMO). Copenhagen, Denmark. https://core.ac.uk/reader/225939220

Iglesias JIP, Navarro E, Alvarez-Jorna E, Armentina I (1992) Feeding, particle selection and absorption in cockles *Cerastoderma edule* (L.) exposed to variable conditions of food concentration and quality. Journal of Experimental Marine Biology and Ecology 162: 177–198. https://doi.org/10.1016/0022-0981(92)90200-T

Iglesias JIP, Urrutia MB, Navarro E, Alvarez-Jorna P, Larretxea X, Bougrier S, Heral M (1996) Variability of feeding processes in the cockle *Cerastoderma edule* (L.) in response to changes in seston concentration and composition. Journal of Experimental Marine Biology and Ecology 197: 121–143. https://doi.org/10.1016/0022-0981(95)00149-2

Iglesias JIP, Urrutia MB, Navarro E, Ibarrola I (1998) Measuring feeding and absorption in suspension-feeding bivalves: An appraisal of the biodeposition method. Journal of Experimental Marine Biology and Ecology 219: 71–86. https://doi.org/10.1016/S0022-0981(97)00175-5

INE (2023) Estatísticas da Pesca: 2022. Lisboa.

Jiang W, Coppola F, Jiang Z, Freitas R, Mao Y, Tan Z, Fang J, Fang J, Zhang Y (2023) A food-web model as a tool for the ecosystem-level management of bivalves in an Atlantic coastal lagoon. Marine Environmental Research 190: 106117. https://doi.org/10.1016/j.marenvres.2023.106117

Jimenez H, Keppel E, Chang AL, Ruiz GM (2018) Invasions in Marine Communities: Contrasting Species Richness and Community Composition Across Habitats and Salinity. Estuaries and Coasts 41: 484–494. https://doi.org/10.1007/s12237-017-0292-4

Jørgensen CB (1989) Water processing in ciliary feeders, with special reference to the bivalve filter pump. Comparative Biochemistry and Physiology. Part A, Physiology 94: 383–394. https://doi.org/10.1016/0300-9629(89)90562-8

Joyce PWS, Kregting LT, Dick JTA (2019) Relative impacts of the invasive Pacific oyster, *Crassostrea gigas*, over the native blue mussel, *Mytilus edulis*, are mediated by flow velocity and food concentration. NeoBiota 45: 19–37. https://doi.org/10.3897/neobiota.45.33116

Karlsson Ö, Jonsson PR, Larsson AI (2003) Do large seston particles contribute to the diet of the bivalve *Cerastoderma edule?* Marine Ecology Progress Series 261: 161–173. https://doi.org/10.3354/meps261161

Katsanevakis S, Wallentinus I, Zenetos A, Leppäkoski E, Çinar ME, Oztürk B, Grabowski M, Golani D, Cardoso AC (2014) Impacts of invasive alien marine species on ecosystem services and biodiversity: A pan-European review. Aquatic Invasions 9: 391–423. https://doi.org/10.3391/ai.2014.9.4.01

Kiørboe T, Møhlenberg F (1981) Particle Selection in Suspension-Feeding Bivalves. Marine Ecology Progress Series 5: 291–296. https://doi.org/10.3354/meps005291

Koo BJ, Seo J (2020) Filtration rates of the manila clam, *Ruditapes philippinarum*, in tidal flats with different hydrographic regimes. PLoS ONE 15: e0228873. https://doi.org/10.1371/journal.pone.0228873

Langdon CJ, Newell RIE (1990) Utilization of detritus and bacteria as food sources by two bivalve suspension-feeders, the oyster *Crassostrea virginica* and the mussel *Geukensia demissa.* Marine Ecology Progress Series 58: 299–310. https://doi.org/10.3354/meps058299

Maia F, Gaspar MB, Barroso CM (2025) Comparative study of *Ruditapes philippinarum* and *Ruditapes decussatus* in Ria de Aveiro, Portugal: Invasive species management and marine resource conservation. Estuarine, Coastal and Shelf Science 314: 109123. https://doi.org/10.1016/j.ecss.2025.109123

Mathers NF (1974) Some comparative aspects of filter-feeding in *Ostrea edulis* L. and *Crassostrea angulata* (Lam.) (Mollusca: Bivalvia). The Journal of Molluscan Studies 41: 89–97. https://doi.org/10.1093/oxfordjournals.mollus.a065265

Møhlenberg F, Riisgård HU (1978) Efficiency of particle retention in 13 species of suspension feeding bivalves. Ophelia 17: 239–246. https://doi.org/10.1080/00785326.1978.10425487

Møhlenberg F, Riisgård HU (1979) Filtration Rate, Using a New Indirect Technique, in Thirteen Species of Suspension-Feeding Bivalves. Marine Biology 54: 143–147. https://doi.org/10.1007/BF00386593

Moura P, Garaulet LL, Vasconcelos P, Chainho P, Costa JL, Gaspar MB (2017) Age and growth of a highly successful invasive species: The manila clam *Ruditapes philippinarum* (Adams & Reeve, 1850) in the Tagus Estuary (Portugal). Aquatic Invasions 12: 133–146. https://doi.org/10.3391/ai.2017.12.2.02

MSFD (2008) MSFD 2008/56/EC. Directive 2008/56/EC of the European parliament and of the council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). http://data.europa.eu/eli/dir/2008/56/oj

Nagai K, Honjo T, Go J, Yamashita H, Oh SJ (2006) Detecting the shellfish killer *Heterocapsa circularisquama* (Dinophyceae) by measuring bivalve valve activity with a Hall element sensor. Aquaculture (Amsterdam, Netherlands) 255: 395–401. https://doi.org/10.1016/j.aquaculture.2005.12.018

Nagasoe S, Suzuki K, Yurimoto T, Fuseya R, Fukao T, Yamatogi T, Kimoto K, Maeno Y (2011) Clearance effects of the pacific oyster *Crassostrea gigas* on the fish-killing algae *Chattonella marina* and *Chattonella antiqua.* Aquatic Biology 11: 201–211. https://doi.org/10.3354/ab00295

Nakamura Y (2001) Filtration rates of the Manila clam, *Ruditapes philippinarum*: Dependence on prey items including bacteria and picocyanobacteria. Journal of Experimental Marine Biology and Ecology 266: 181–192. https://doi.org/10.1016/S0022-0981(01)00354-9

Navarro E, Iglesias JIP (1993) Infaunal filter-feeding bivalves and the physiological response to short-term fluctuations in food availability and composition. In: Dame RF (Ed.) Bivalve Filter Feeders. Heidelberg: Springer, Berlin, 25–56. https://doi.org/10.1007/978-3-642-78353-1_2

Navarro JM, Widdows J (1997) Feeding physiology of *Cerastoderma edule* in response to a wide range of seston concentrations. Marine Ecology Progress Series 152: 175–186. https://doi.org/10.3354/meps152175

Navarro E, Iglesias JIP, Ortega MM (1992) Natural sediment as a food source for the cockle *Cerastoderma edule* (L.): Effect of variable particle concentration on feeding, digestion and the scope for growth. Journal of Experimental Marine Biology and Ecology 156: 69–87. https://doi.org/10.1016/0022-0981(92)90017-5

Nielsen M, Hansen BW, Vismann B (2017) Feeding traits of the European flat oyster, *Ostrea edulis*, and the invasive Pacific oyster, *Crassostrea gigas.* Marine Biology 164: 1–10. https://doi.org/10.1007/s00227-016-3041-5

Nilin J, Pestana JLT, Ferreira NG, Loureiro S, Costa-Lotufo LV, Soares AM (2012) Physiological responses of the European cockle *Cerastoderma edule* (Bivalvia: Cardidae) as indicators of coastal lagoon pollution. The Science of the Total Environment 435: 44–52. https://doi.org/10.1016/j.scitotenv.2012.06.107

NIPOGES (2022) Relatório Final - Estado atual das populações de amêijoa-japonesa da Ria de Aveiro, lagoa de Óbidos e estuários do Tejo e Sado – Bases científicas para uma gestão sustentável do recurso.

Ong EZ, Briffa M, Moens T, Van Colen C (2017) Physiological responses to ocean acidification and warming synergistically reduce condition of the common cockle *Cerastoderma edule.* Marine Environmental Research 130: 38–47. https://doi.org/10.1016/j.marenvres.2017.07.001

Pascoe PL, Parry HE, Hawkins AJS (2009) Observations on the measurement and interpretation of clearance rate variations in suspension-feeding bivalve shellfish. Aquatic Biology 6: 181–190. https://doi.org/10.3354/ab00123

Pernet F, Tremblay R, Redjah I, Sévigny JM, Gionet C (2008) Physiological and biochemical traits correlate with differences in growth rate and temperature adaptation among groups of the eastern oyster *Crassostrea virginica.* The Journal of Experimental Biology 211: 969–977. https://doi.org/10.1242/jeb.014639

Petersen JK, Bougrier S, Smaal AC, Garen P, Robert S, Larsen JEN, Brummelhuis E (2004) Intercalibration of mussel *Mytilus edulis* clearance rate measurements. Marine Ecology Progress Series 267: 187–194. https://doi.org/10.3354/meps267187

Pranovi F, Franceschini G, Casale M, Zucchetta M, Torricelli P, Giovanardi O (2006) An ecological imbalance induced by a non-native species: The Manila clam in the Venice Lagoon. Biological Invasions 8: 595–609. https://doi.org/10.1007/s10530-005-1602-5

Prins TC, Smaal AC, Pouwer AJ (1991) Selective ingestion of phytoplankton by the bivalves *Mytilus edulis* L. and *Cerastoderma edule* (L.). Hydrological Bulletin 25: 93–100. https://doi.org/10.1007/BF02259595

Rahman MA, Henderson S, Miller-Ezzy PA, Li XX, Qin JG (2020) Analysis of the seasonal impact of three marine bivalves on seston particles in water column. Journal of Experimental Marine Biology and Ecology 522: 151251. https://doi.org/10.1016/j.jembe.2019.151251

Ramajal J, Picard D, Costa JL, Carvalho FB, Gaspar MB, Chainho P (2016) Amêijoa-japonesa, uma nova realidade no estuário do Rio Tejo: Pesca e pressão social e impacto socio-económico. Entre Rios e Mares: um Património de Ambientes, Histórias e Saberes. Tomo V da Rede BrasPor.

Riisgård HU (2001) On measurement of filtration rates in bivalves—the stony road to reliable data: Review and interpretation. Marine Ecology Progress Series 211: 275–291. https://doi.org/10.3354/meps211275

Rodrigues N, Ribeiro D, Miyahira IC, Portugal SGM, Santos LN, Neves RAF (2023) Do feeding responses of a non-native bivalve outperform the native one in a coastal lagoon? A possible explanation for the invasion success of the dark false mussel *Mytilopsis leucophaeata*. PeerJ 11: e15848. https://doi.org/10.7717/peerj.15848

Rosa M, Ward JE, Shumway SE (2018) Selective Capture and Ingestion of Particles by Suspension-Feeding Bivalve Molluscs: A Review. Journal of Shellfish Research 37: 727–746. https://doi.org/10.2983/035.037.0405

Ruano F, Sobral DV (2000) Marine non-indigenous species – current situation in Portugal. In: Rodrigues L, Reino L, Godinho LO, Freitas H (Eds) Proceedings of the 1st Symposium on Non-indigenous Species: Introduction, Causes and Consequences. Liga para a Protecção da Natureza, Lisboa, Portugal, 58–63.

Ruiz GM, Fofonoff P, Hines AH, Grosholz ED (1999) Non-indigenous species as stressors in estuarine and marine communities: Assessing invasion impacts and interactions. Limnology and Oceanography 44: 950–972. https://doi.org/10.4319/lo.1999.44.3_part_2.0950

Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ, Hines AH (2000) Invasion of Coastal Marine Communities in North America: Apparent Patterns, Processes, and Biases. Annual Review of Ecology and Systematics 31: 481–531. https://doi.org/10.1146/annurev.ecolsys.31.1.481

Ruiz GM, Freestone AL, Fofonoff PW, Simkanin C (2009) Habitat Distribution and Heterogeneity in Marine Invasion Dynamics: the Importance of Hard Substrate and Artificial Structure. In: Wahl M (Ed.) Marine Hard Bottom Communities. Springer-Verlag, Berlin, 321–332. https://doi.org/10.1007/b76710_23

Shimeta J, Jumars PA (1991) Physical mechanisms and rates of particle capture by suspension-feeders. Oceanography and Marine Biology 29: 191–257.

Shinen JS, Morgan SG (2009) Mechanisms of invasion resistance: Competition among intertidal mussels promotes establishment of invasive species and displacement of native species. Marine Ecology Progress Series 383: 187–197. https://doi.org/10.3354/meps07982

Smaal AC, van Duren LA (2019) Bivalve Aquaculture Carrying Capacity: Concepts and Assessment tools. In: Smaal A, Ferreira J, Grant J, Petersen J, Strand Ø (Eds) Goods and Services of Marine Bivalves. Springer International Publishing, 451–483. https://doi.org/10.1007/978-3-319-96776-9_23

Smaal AC, Vonck APMA, Bakker M (1997) Seasonal variation in physiological energetics of *Mytilus edulis* and *Cerastoderma edule* of different size classes. Journal of the Marine Biological Association of the United Kingdom 77: 817–838. https://doi.org/10.1017/S0025315400036213

Sobral P, Widdows J (1997) Influence of hypoxia and anoxia on the physiological responses of the clam *Ruditapes decussatus* from southern Portugal. Marine Biology 127: 455–461. https://doi.org/10.1007/s002270050033

Sobral P, Widdows J (2000) Effects of increasing current velocity, turbidity and particle-size selection on the feeding activity and scope for growth of *Ruditapes decussatus* from Ria Formosa, southern Portugal. Journal of Experimental Marine Biology and Ecology 245: 111–125. https://doi.org/10.1016/S0022-0981(99)00154-9

Sonier R (2017) Rôle nutritionnel du picophytoplancton pour les bivalves d'élevage. PHD Thesis. Université du Québec à Rimouski (Rimouski). https://semaphore.uqar.ca/id/eprint/1359/

Steeves L, Vimond C, Strohmeier T, Casas S, Strand Ø, Comeau LA, Filgueira R (2022) Relationship between pumping rate and particle capture efficiency in three species of bivalves. Marine Ecology Progress Series 691: 55–68. https://doi.org/10.3354/meps14063

Steger J, Bošnjak M, Belmaker J, Galil BS, Zuschin M, Albano PG (2022) Non-indigenous molluscs in the Eastern Mediterranean have distinct traits and cannot replace historic ecosystem functioning. Global Ecology and Biogeography 31: 89–102. https://doi.org/10.1111/geb.13415

Stenton-Dozey JME, Brown AC (1992) Clearance and retention efficiency of natural suspended particles by the rock-pool bivalve *Venerupis corrugatus* in relation to tidal availability. Marine Ecology Progress Series 82: 175–186. https://doi.org/10.3354/meps082175

Stenton-Dozey JME, Brown AC (1994) Short-term changes in the energy balance of *Venerupis corrugatus* (Bivalvia) in relation to tidal availability of natural suspended particles. Marine Ecology Progress Series 103: 57–64. https://doi.org/10.3354/meps103057

Stiger-Pouvreau V, Thouzeau G (2015) Marine Species Introduced on the French Channel-Atlantic Coasts: A Review of Main Biological Invasions and Impacts. Open Journal of Ecology 5: 227–257. https://doi.org/10.4236/oje.2015.55019

Streftaris N, Zenetos A, Papathanassiou E (2005) Globalisation in marine ecosystems: The story of non-indigenous marine species across European seas. Oceanography and Marine Biology - an Annual Review 43: 419–453. https://doi.org/10.1201/9781420037449.ch8

Strohmeier T, Strand Ø, Alunno-Bruscia M, Duinker A, Cranford PJ (2012) Variability in particle retention efficiency by the mussel *Mytilus edulis.* Journal of Experimental Marine Biology and Ecology 412: 96–102. https://doi.org/10.1016/j.jembe.2011.11.006

Stuart V, Klumpp DW (1984) Evidence for food-resource partitioning by kelp-bed filter feeders. Marine Ecology Progress Series 16: 27–37. https://doi.org/10.3354/meps016027

Tamayo D, Ibarrola I, Navarro E (2013) Thermal dependence of clearance and metabolic rates in slow- and fast-growing spats of manila clam *Ruditapes philippinarum.* Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology 183: 893–904. https://doi.org/10.1007/s00360-013-0764-1

Troost K, Stamhuis EJ, van Duren LA, Wolff WJ (2009) Feeding current characteristics of three morphologically different bivalve suspension feeders, *Crassostrea gigas*, *Mytilus edulis* and *Cerastoderma edule*, in relation to food competition. Marine Biology 156: 355–372. https://doi.org/10.1007/s00227-008-1088-7

Truhlar AM, Dodd JA, Aldridge DC (2014) Differential leaf-litter processing by native (*Gammarus pulex*) and invasive (*Dikerogammarus villosus*) freshwater crustaceans under environmental extremes. Aquatic Conservation 24: 56–65. https://doi.org/10.1002/aqc.2375

Urrutia MB, Iglesias JIP, Navarro E (1997) Feeding behaviour of *Cerastoderma edule* in a turbid environment: Physiological adaptations and derived benefit. Hydrobiologia 355: 173–180. https://doi.org/10.1023/A:1003050700881

Walne PR, Mann R (1975) Growth and biochemical composition in *Ostrea edulis* and *Crassostrea gigas*. In: Barnes H (Ed.) Ninth European marine biology symposium. Aberdeen University Press Scotland, United Kingdom, 587–607.

Ward JE, Sanford LP, Newell RIE, MacDonald BA (1998) A new explanation of particle capture in suspension-feeding bivalve molluscs. Limnology and Oceanography 43: 741–752. https://doi.org/10.4319/lo.1998.43.5.0741

Widdows J (2001) Bivalve clearance rates: Inaccurate measurements or inaccurate reviews and misrepresentation. Marine Ecology Progress Series 221: 303–305. https://doi.org/10.3354/meps221303

Widdows J, Navarro JM (2007) Influence of current speed on clearance rate, algal cell depletion in the water column and resuspension of biodeposits of cockles (*Cerastoderma edule*). Journal of Experimental Marine Biology and Ecology 343: 44–51. https://doi.org/10.1016/j.jembe.2006.11.011

WFD (2000) WFD, 2000/60/EC. Directive 2000/60/EC of the European Parliament of the Council of 23 October 2000 establishing a framework for community action in the field of water policy (Water Framework Directive). http://data.europa.eu/eli/dir/2000/60/oj

Yu Z, Zhou Y, Qi Z, Luo P, Hu C (2017) Temporal dynamics in clearance rate of the Portuguese oyster *Crassostrea angulata* cultivated in Dapeng Cove, southern China. Aquaculture (Amsterdam, Netherlands) 479: 824–828. https://doi.org/10.1016/j.aquaculture.2017.07.030

Zaiko A, Daunys D (2015) Invasive ecosystem engineers and biotic indices: Giving a wrong impression of water quality improvement? Ecological Indicators 52: 292–299. https://doi.org/10.1016/j.ecolind.2014.12.023

Zorita I, Solaun O, Borja A, Franco J, Muxika I, Pascual M (2013) Spatial distribution and temporal trends of soft-bottom marine benthic alien species collected during the period 1989-2008 in the Nervión estuary (southeastern Bay of Biscay). Journal of Sea Research 83: 104–110. https://doi.org/10.1016/j.seares.2013.04.009

Supplementary material 1

Relationship between the Suspended Particulate Matter (SPM) and the turbidity for the field experiments site (an aquaculture farm located in the Sado estuary, Setúbal, Portugal)

Authors: Sara Cabral, Frederico Carvalho, Joana P. C. Cruz, Joshua Heumüller, Jose M. F. Babarro, Luc A. Comeau, Paula Chainho, Ana C. Brito

Data type: pdf

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.102.148326.suppl1

Supplementary material 2

Representation for a single incubator with a bivalve actively filtering

Authors: Sara Cabral, Frederico Carvalho, Joana P. C. Cruz, Joshua Heumüller, Jose M. F. Babarro, Luc A. Comeau, Paula Chainho, Ana C. Brito

Data type: pdf

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.102.148326.suppl2

Supplementary material 3

Representation for both a sample with bivalve (green) and the control (grey) of (A) the decline in the number of particles over the experiment time and (B) the linear regression between the particle concentration (transformed in natural logarithm) and the elapsed time

Authors: Sara Cabral, Frederico Carvalho, Joana P. C. Cruz, Joshua Heumüller, Jose M. F. Babarro, Luc A. Comeau, Paula Chainho, Ana C. Brito

Data type: pdf

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.102.148326.suppl3

Supplementary material 4

PERMANOVA analysis results on capture efficiency (CE) of three bivalve species (*C. edule*, *M. angulata* and *R. philippinarum*)

Authors: Sara Cabral, Frederico Carvalho, Joana P. C. Cruz, Joshua Heumüller, Jose M. F. Babarro, Luc A. Comeau, Paula Chainho, Ana C. Brito

Data type: pdf

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.102.148326.suppl4

Supplementary material 5

PERMANOVA Pair-wise test to detect differences on CE between particle sizes for field experiments of three bivalve species (*C. edule*, *M. angulata* and *R. philippinarum*)

Authors: Sara Cabral, Frederico Carvalho, Joana P. C. Cruz, Joshua Heumüller, Jose M. F. Babarro, Luc A. Comeau, Paula Chainho, Ana C. Brito

Data type: pdf

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.102.148326.suppl5

Supplementary material 6

PERMANOVA Pair-wise test to detect differences on CE between particle sizes for laboratory experiments of three bivalve species (*C. edule*, *M. angulata* and *R. philippinarum*)

Authors: Sara Cabral, Frederico Carvalho, Joana P. C. Cruz, Joshua Heumüller, Jose M. F. Babarro, Luc A. Comeau, Paula Chainho, Ana C. Brito

Data type: pdf

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.102.148326.suppl6

Supplementary material 7

Relationship between the Condition Index (Spearman correlation test, $p < 0.05$) and the Clearance Rate (CR) for field (A) and laboratory (B) experiments of three bivalve species (*C. edule*, *M. angulata* and *R. philippinarum*)

Authors: Sara Cabral, Frederico Carvalho, Joana P. C. Cruz, Joshua Heumüller, Jose M. F. Babarro, Luc A. Comeau, Paula Chainho, Ana C. Brito

Data type: pdf

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.102.148326.suppl7

Supplementary material 8

Average and maximum density (individuals per m2) and biomass (g per m2) of three bivalve species (*C. edule*, *M. angulata* and *R. philippinarum*) and all bivalves from the soft-sediment communities in both Sado and Tagus estuaries in 2018

Authors: Sara Cabral, Frederico Carvalho, Joana P. C. Cruz, Joshua Heumüller, Jose M. F. Babarro, Luc A. Comeau, Paula Chainho, Ana C. Brito

Data type: docx

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.102.148326.suppl8